

Ecological strategies and population regulation of Collembola in heterogeneous environments

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With 9 figures

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1. Life history of Collemboles in general

Collembola or springtails belong with mites (Acari) to the most abundant and widespread groups of soil arthropods, both in terms of individuals and species. The surface dwelling species *Orchesella cincta* (L.) and *Tomocerus minor* (Lubbock), on which attention is focussed here, reach about 5 mm in length. The structure from which their common name is derived, the springtail or furcula, is strongly developed (Fig. 1) and is involved in the important escape-reaction from predation (ERNSTING & JANSEN 1978; CHRISTIAN 1978; SIMON 1969). As an archaic group of species (the oldest discoveries are from the Devonian) the Collembola have several unique traits. The development is epimetabolic, that is differentiation occurs gradually during development. They moult throughout their lives and are able to replace broken appendages during this process (SWEETMAN 1934). The animals become sexually mature and start to reproduce after about ten moults (LINDENMANN 1950; JOOSSE & VELTKAMP 1970). Moulting continues after sexual maturity has been reached and the total number of moults thus depends

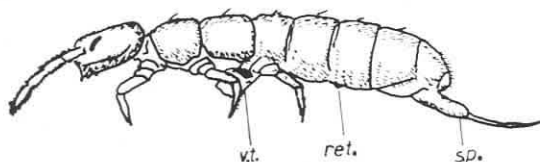


Fig. 1. Representative of the Collembola. v. t. = ventral tube; ret. = retinaculum; sp. = springtail (furcula).

on the longevity of the animals; up to 37 have been recorded for *O. cincta* (LINDENMANN 1950). There is a strong rhythmicity of non-reproductive and reproductive instars; the duration of the non-reproductive instars being somewhat shorter than that of the reproductive instars (JOOSSE et al. 1973). During a reproductive instar the females are receptive for at the most the first 48 hours. After uptake of one or more spermatophores they start to produce eggs within 2—3 hours. The males produce spermatophores throughout the instar (Fig. 2). An instar takes about 4—5 days (at 20 °C). Feeding occurs during only 3 days, because during the premoult, which takes 2 days, the renovation of the mid-gut epithelium is prepared (JOOSSE & TESTERINK 1977a), and the animals do not feed (DE WIT & JOOSSE 1971). Moulting and reproduction take place in aggregations (JOOSSE & VERHOEF 1974) in the formation of which environmental factors, especially moisture, work together with aggregation pheromones (VERHOEFF et al. 1977a, b). It is interesting to note that feeding after a starvation period synchronizes a population in this moulting and reproduction rhythm, which is a very useful phenomenon for experimental work (JOOSSE & VELTKAMP 1970; JOOSSE & VERHOEF 1974).

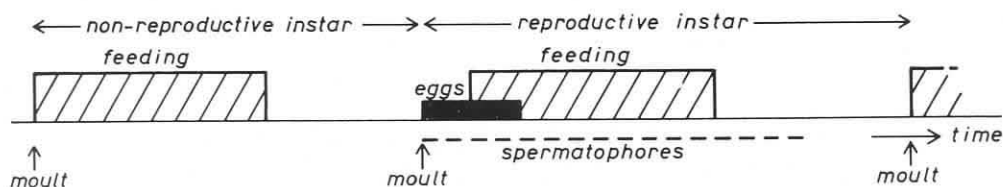


Fig. 2. Feeding and reproductive activities during the moult cycle.

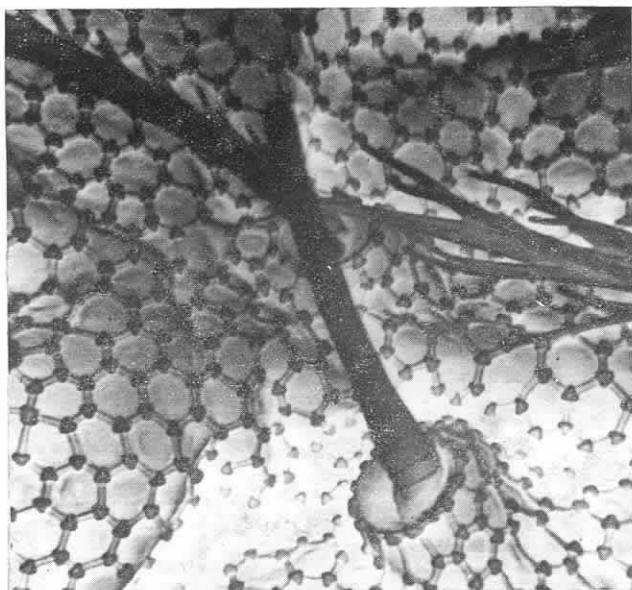


Fig. 3. Cuticle structure of *Orchesella cineta* ($\times 16,000$, SEM photo by VERHOEF).

Most Collembola are restricted to the soil environment, because of their low resistance to desiccation. Some species can be found occasionally on plants and tree bark (BOWDEN et al. 1976; BAUER 1979), and only a few species are able to live in more exposed areas. This sensitivity to desiccation is demonstrated in the morphology and physiology. The thin-walled cuticle is a compromise between a barrier to desiccation and an organ for respiration, since a tracheal system is absent. In Fig. 3 it is shown that the cuticle has in parts permeability barriers, ring-shaped structures with a wax layer (LAWRENCE & MASSOUD 1973; GHIRADELLA & RADIGAN 1974; BARRA 1977), and elsewhere deeper areas, where presumably a relatively high humidity is maintained and where gas exchange can occur without too much water loss. This structure is absent in the ventral tube (EISENBEIS 1974), a thin walled appendage of the first abdominal segment (Fig. 1). It is always moist and therefore very suitable for gas exchange and because of its retractability, water loss and consequently the ionic concentration of the blood, can be regulated (NOBLE-NESBITT 1963; EISENBEIS 1974, 1979).

In their physiology these animals exhibit a strong economy with respect to water. Their metabolic waste products are not removed by Malpighian tubules, which are absent, but are partly stored in the ductless cephalic and abdominal nephridia (HUMBERT 1975) with a minimum of water loss and partly removed by ultrafiltration-reabsorption kidneys, the labial nephridia (VERHOEF et al. 1979). Furthermore the mid-gut epithelium plays an important rôle in periodic storage-excretion. These epithelium-cells are regularly shed, for each moult involves a total renewal of the gut epithelium. The old cells are repleted with excretory material (Fig. 4) and are considered to be accumulators of foreign and excess ions (HUMBERT 1978).

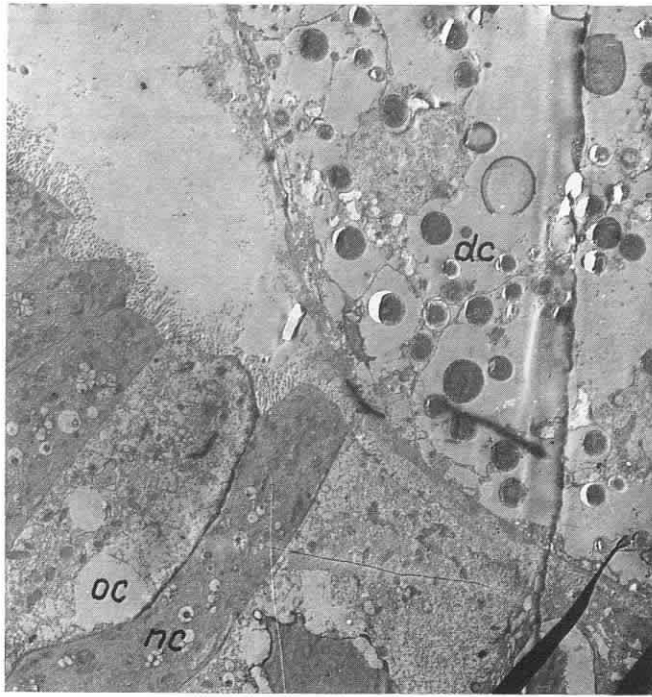


Fig. 4. Mid-gut epithelium of *Orchesella cincta* during regeneration ($\times 4,900$). o. c. = old cells; n. c. = new cells; d. c. = degenerated cells (slough).

In experiments on feeding of Collembola with lead contaminated food, it was found that this mechanism of intestinal excretion can remove as much as 44% of the lead within two moults (Joosse & BUKER 1979).

The water economy and restriction of these animals to the soil environment suggest that water availability is an important factor in survival and thus in distribution and abundance. In the present paper an attempt is made to relate the divergent survival strategies of two coexistent species *O. cincta* and *T. minor*, with respect to variable humidity, to their distribution and abundance in the field.

2. Population dynamics and moisture availability

The relation of population numbers and moisture availability was studied in 15 species of litter dwelling Collembola in 8 different forest habitats in Holland, during 4 years. In four of these habitats the species *O. cincta* and *T. minor* coexist. The areas are very different in soil composition and structure, two of them are situated on fine-grained clay and silt, the other two on sand. The sandy areas are wooded with pine (*Pinus sylvestris*) and birch (*Betula* spec.) respectively, the clay and silty areas are planted with oak (*Quercus rubra*) and with poplar (*Populus* spec.) respectively. The sandy and clay habitats show a very different pattern of moisture distribution in the litter and also in water availability during the seasons. The humidity variations in the litter from two of the habitats, for 1973 to 1976, are illustrated graphically in Fig. 5. It can be seen that the water content of the oak plantation on clay is much less variable during the season than that of the pine plantation. Moreover, the variability in the moisture content of the 24 litter samples of one date is greater each month, in the pine forest than in the oak plantation, as is shown by the standard errors. In Table 1 this variability is expressed as the ratio s^2/m of the samples taken at the various points in time and the

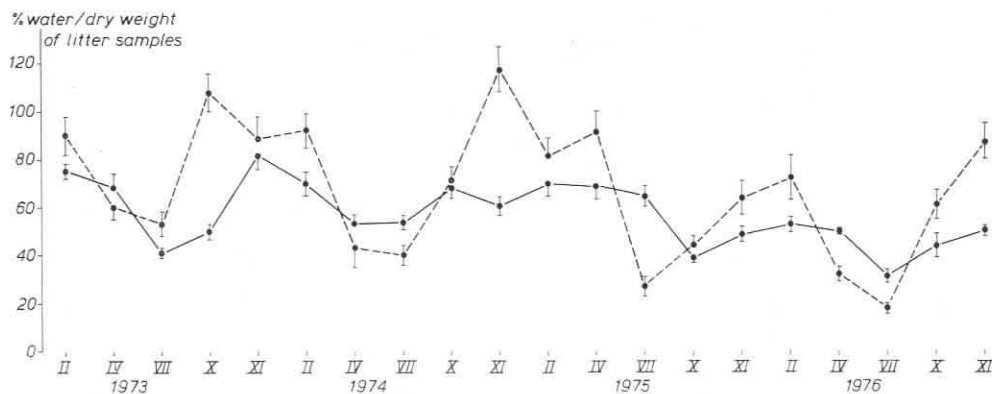


Fig. 5. Seasonal water content of litter samples from an oak plantation on clay (—) and a pine plantation on sand (---). The data indicate the mean value of 24 samples with S.E.

Table 1. Humidity variation (s^2/m) in time and space and population numbers of *O. cincta* and *T. minor* in four sampling areas

Habitat	Humidity variation ¹⁾		Mean number/m ²	
	in time	in space	<i>O. cincta</i>	<i>T. minor</i>
Oak-clay	3.14	5.45	22.8	872.6
Poplar-silt	6.42	4.29	117.8	425.2
Pine-sand	11.34	15.39	286.1	37.7
Birch-sand	12.47	8.97	262.2	92.4

¹⁾ for explanation, see text.

mean s^2/m of the 24 samples per point in time and compared to the population numbers of both species. It can be seen that on fine-grained soils the humidity variation in space and time is less than on sandy soils. In the situations with relatively low variation *T. minor* dominates, whereas in sandy sites with high humidity variations *O. cincta* dominates. Apparently these two species possess different properties with respect to an important difference between these habitats, which is suggested to be the variation in humidity.

3. Physiological properties and water availability

The different properties concerning water relations between the two species become apparent from desiccation experiments. The mean survival (LD_{50} in a very dry situation of 60% R. H. and 20 °C) was about 6 hours (367 min.) in *O. cincta*, whereas 50% of *T. minor* died within 40 min. It can be concluded that *O. cincta* is much more resistant to desiccation than *T. minor*.

The causes of these differences can be analysed by measuring the transpiration rate of an individual under fixed humidity conditions. This has been done with the aid of a very sensitive Cahn electrobalance, with which the decrease in weight of animals was measured in controlled humidity conditions created by salt solutions or silica gel (VANNIER 1973a, b; VERHOEF 1978; VERHOEF & WITTEVEEN 1980). In Fig. 6 it is shown that the normal transpiration rate of *O. cincta* is about 10 times lower than that of *T. minor*. After death the transpiration rate in *O. cincta* increases, which suggests a regulation mechanism in living individuals. This phenomenon is absent in *T. minor*.

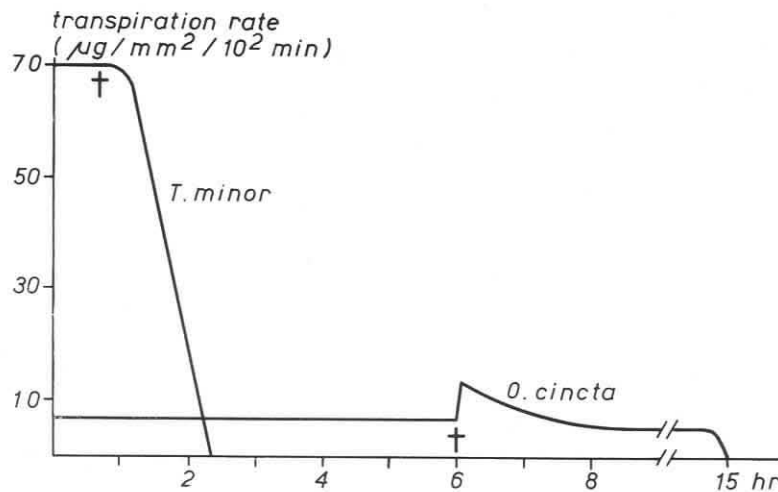


Fig. 6. The transpiration rate of *Orchesella cincta* and *Tomocerus minor* at 18 °C and 65 °C R. H. (after VERHOEF 1978). + = point of death.

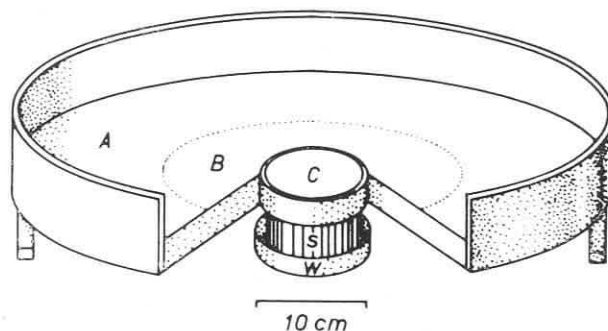


Fig. 7. Test arena with heterogeneous water and food conditions. C = central disc with water supply (w.) and sponge (s); A = dry area with food; B = dry area without food (after VERHOEF & NAGELKERKE 1977).

4. Behavioural aspects with respect to water availability

The behavioural consequences of differences in physiological ability to withstand drought have been demonstrated in a laboratory experiment (VERHOEF & NAGELKERKE 1977). The artificial heterogeneous habitat consisted of a plaster of Paris substrate in the centre of which water was supplied from a reservoir by means of a sponge (Fig. 7, part C). The areas A and B in the arena were completely dry: A was provided with dried *Pleurococcus* (green algae) as food. A hundred individuals of each species were introduced into the box and remained there for 6 days. The distribution of the individuals in the box after 6 days is shown in Table 2, from which it is apparent that nearly all individuals of *T. minor* could be found on the moist part, whereas *O. cincta* could be found everywhere, mainly on the dry food, but also in the dry area. Eggs were laid by both species only on the moist centre. Freshly laid eggs absorb water by which they increase in size (SCHALLER 1970). The significance of the ability of *O. cincta* to leave the moist area, becomes clear from Fig. 8, where a group of synchronized individuals of *O. cincta* is followed with respect to its distribution in an arena with a moist centre and a dry food-ring. Before ecdysis, all the animals leave the dry food and transfer to the moist area, where they remain to moult and to lay their eggs. Afterwards they return to the dry area to feed.

Table 2. Distribution of 100 individuals of *O. cincta* and *T. minor* after 6 days in an arena with moist (C), dry (B) and food (A) areas (after VERHOEF & NAGELKERKE 1977)

	<i>O. cincta</i>	<i>T. minor</i>
on moist (C)	20 %	95 %
on dry (B)	23 %	2 %
on food (A)	57 %	3 %

Thus thanks to its low transpiration rate, *O. cincta* is able to commute between water and food, and can, therefore, better survive in this heterogeneous habitat since it extends its range into dry areas. *T. minor* is unable to do so and thus starves. Field data on locomotion indicate a higher activity in *O. cincta* and indicate that this different behaviour also occurs in natural conditions (Joosse 1971).

5. Predation and soil moisture

It is well-known that Collembola are commonly prey to a great number of predators (SIMON 1964; ERNSTING & JOOSSE 1974). In pieces of forest floor with their natural fauna, kept in climate rooms, radioactively labelled Collembola of the two species were introduced. After 3 weeks the plots were carefully searched and all the animals were collected and scanned for radioactivity. It became apparent that 40 different predatory species, belonging to carabids, staphylinids and araneids, had eaten radioactive prey.

A more detailed analysis of the predation process clearly demonstrated that movement by the springtail increases the risk of being seized by a predator (ERNSTING et al. 1977; ERNSTING & JANSSEN 1978). Locomotory activity of Collembola is, however, considerable influenced by drought (Joosse & GROEN 1970). All species show, as an escape-reaction, an increased activity with a decrease in humidity. This could mean that the negative physiological

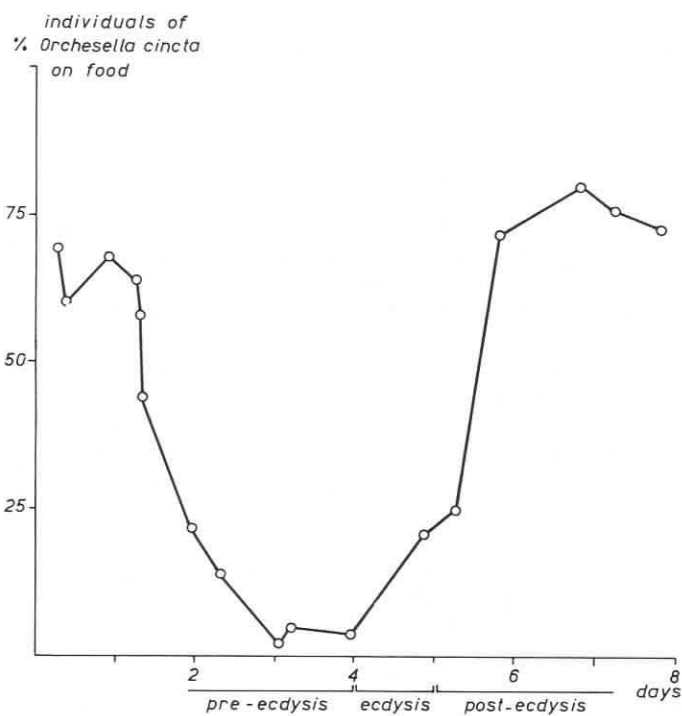


Fig. 8. Percentage of synchronized *Orchesella cincta* present in the dry area with food during a moulting instar (after VERHOEF & NAGELKERKE 1977).

Table 3. Locomotory activity of *O. cineta* and *T. minor* and median of the number of unsuccessful attacks by the predator *Notiophilus biguttatus* [Carabidae] in dry and wet environments.

	<i>O. cineta</i>		<i>T. minor</i>	
	mean activity (%)	median unsuccessful attacks	mean activity (%)	median unsuccessful attacks
dry	43—70	4	6—11	2
wet	24—46	1	0—9	1

Loc. act. expressed as % of maximum possible activity; after ERNSTING 1978.

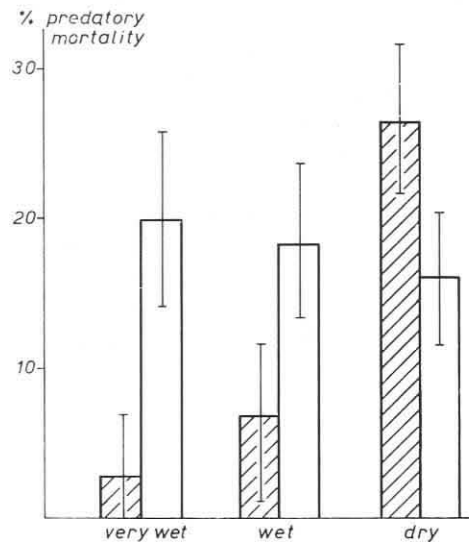


Fig. 9. Predation on *Orchesella cineta* (blank columns) and *Tomocerus minor* (hatched columns) (\pm S.E.) in different humidity conditions (after ERNSTING 1978).

effect of drought coincides with a high predation risk. In an experiment predation risk was studied in a very wet, a wet and a dry environment over a period of 8 days (ERNSTING 1978) using the predator *Notiophilus gibuttatus* F. (Carabidae). From Fig. 9 it appears that the predation risk of *T. minor* was significantly higher in the dry environment. For *O. cineta* however, the risk was similar in all environments. An explanation for this difference was offered by ERNSTING (1978) on the basis of findings and summarized in Table 3. In the relevant experiments, the number of unsuccessful attacks of the predator was observed. Although the locomotory activity of *O. cineta*, being much higher than that of *T. minor*, makes it more vulnerable to predation, it is clear that under dry conditions *O. cineta* has a much greater ability to escape from a predator. This ability must be attributed to greater alertness and readiness to escape using the jumping mechanism.

6. Reproduction and water availability

Reproduction and feeding are directly linked. When Collembola are starved, they immediately stop important activities such as moulting and locomotion and the production of eggs (JOOSSE & TESTERINK 1977a). In several studies of the nutritional condition of Collembola in the field, considerable numbers of individuals were found with empty guts (BÖDVARSSON 1970, 1973; JOOSSE 1975; MURALEEDHARAN & PRABHOO 1978). The question is, whether these empty guts can be interpreted as an indication of starvation. Empty guts can

to a certain extent be accounted for by the frequent moults (see section 1). However, many individuals of *O. cineta* with empty guts, which were found in the field during dry periods in several summers (JOSSE & TESTERINK 1977b), appeared to be in a real starved condition, since the glycogen and fat contents of the bodies were very low (TESTERINK 1981a). Probably food was scarce at such times, or at any rate, feeding activity was arrested.

Starved *O. cineta* specimens demonstrate a relatively longer survival than fully-fed animals and thus seem to be adapted to food scarcity (JOSSE & TESTERINK 1977a). They protect themselves by reducing energy-demands: by stopping egg-production, moulting and locomotory activity, thus increasing the chance of survival and reproductive success in the future. After a temporary drought, feeding and other activities restart simultaneously, resulting in, as previously mentioned, synchronized moulting and reproduction. A rapid increase in population numbers is found after an unfavourable period (JOSSE 1975; JOSSE & TESTERINK 1977b).

It is interesting that these phenomena could only been demonstrated in *O. cineta* and appear to be absent in *T. minor* (TESTERINK 1981b). The latter species seems to be unable to delay its reproduction until more favourable times and is, therefore, eliminated when humidity conditions become critical (VERHOEF & VAN SELM 1978).

7. Conclusions and discussions

In a habitat where moisture is heterogeneously distributed and wet and dry seasons alternate and where *O. cineta* and *T. minor* co-exist, *Orchesella* dominates (Table 1). Such a habitat, although unstable, is favourable for this species thanks to its various abilities (Table 4): 1. physiological resistance to desiccation; 2. high mobility between wet and dry areas; 3. ability to escape predators; 4. flexible reproduction.

Relative humidity is clearly the principal environmental variable to which this set of abilities is directed.

Table 4. Various adaptations and the suggested effects on the population numbers of *O. cineta* and *T. minor* in heterogeneous environments

Adaptation	<i>O. cineta</i>	<i>T. minor</i>
resistance to desiccation	+	—
commuting behaviour	+	—
escape from predation	+	—
flexible reproduction	+	—

Particular attention is focussed on the ability of *O. cineta* to regulate reproductive efforts in response to unpredictable moisture conditions, resulting in an adjustment of reproductive timing to favourable conditions. This synchronization, which assures reproductive success, has several population ecological aspects. Firstly, the population avoids wasting its energy and the high numbers of offspring produced after unfavourable times restore the population size (GIESEL 1976). Secondly, the synchronization may have implications for predation: the synchronous unpredictable surge in reproduction floods the environment with a large number of young. It may be impossible for a predator to consume a large fraction of the available prey (WILBUR et al. 1974).

A further positive influence of spatial heterogeneity on the population numbers of *O. cineta* may be found in consequences of the commuting ability of this species. It can possibly select areas with food, but also sheltered areas, which may reduce the risk of predation (ERNSTING 1978) and the intensity of competition (SMITH 1972). From laboratory experiments it emerged that when suitable space to lay eggs and to moult is restricted, *O. cineta* is excluded from these areas by *T. minor* (VERHOEF, unpubl.).

These phenomena may partly explain the lower success of *O. cineta* in a homogeneous and stable environment, where its abilities are of less value. Moreover, in a wetter situation *O.*

cineta appeared to be more commonly predated (Fig. 9): the average predation risk in a homogeneous environment is possibly higher.

The rôle of processes in regulating the population size of these species apparently depends on the relative favourability of the environment. This finding is in agreement with the ideas of the comprehensive school (KREBS 1978). It is suggested that in an unstable environment, clearly less favourable for *T. minor*, mainly density-independent factors, such as relative humidity in this case, affect population numbers. The same habitat is more favourable for *O. cineta*: humidity is important, but acts indirectly on the numbers via mobility and predation. In a more stable and favourable environment biotic factors could play a more direct rôle: a higher predation risk for *O. cineta* and especially stronger competition between the two species.

8. Acknowledgements

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9. Summary · Zusammenfassung

A comparison of the population numbers of the Collembola species *Orchesella cineta* (L.) and *Tomocerus minor* (LUBBOCK) over a period of 4 years in 4 sites showed marked differences between species and sites. The differences could be attributed to the various adaptations of the species i.e. physiological resistance to desiccation, use of the habitat, ability to escape predators and flexibility in reproduction. It was shown that the population changes are influenced by an interacting complex of biotic and physical factors, which vary according to the favourability of the environment for the species concerned.

Ökologische Strategien und Populationsdynamik von Collembolen in heterogener Umwelt

Die Populationsdichte der Collembolen *Orchesella cineta* (L.) und *Tomocerus minor* (LUBBOCK) zeigte über eine Beobachtungsperiode von 4 Jahren an 4 Standorten große Unterschiede zwischen Arten und Standorten. Diese Unterschiede werden als unterschiedliche Anpassungsstrategien interpretiert: (1) physiologische Austrocknungsresistenz, (2) Raum- und Nahrungsnutzung, (3) Meidung von Predatoren und (4) Reproduktionsflexibilität.

Die Populationsdichte wird beeinflusst von einem Komplex biotischer und physischer Faktoren, abhängig von der Eignung des Standortes für die Art.

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